SOME ASPECTS OF DIAPAUSE IN THE FIELD CRICKETS *PTERONEMOBIUS NIGROVUS* AND *P. BIGELOWI* (ORTHOPTERA: NEMOBIINAE), WITH NOTES ON THEIR ECOLOGY

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ABSTRACT

The small, black field crickets, *Pteronemobius nigrovus* and *P. bigelowi* are common in grasslands throughout New Zealand. The latter appears to predominate in the north of the North Island whereas the former is most common in the south and in alpine areas. Egg incubation time and hatching success of eggs of both species were examined in the laboratory under several temperature regimes. Both species possess a facultative egg diapause which appears to be a device for escaping extreme winter cold. It is suggested that egg diapause is polygenically controlled and modified by environmental factors such as photoperiod and temperature.

INTRODUCTION

The small, black field crickets, *Pteronemobius nigrovus* Swan, 1972 and *P. bigelowi* Swan, 1972 are distributed widely in grasslands throughout New Zealand. Some aspects of their biology have been reported by Wilkinson (1970), Parkes (1972) and Swan (1972) and the present author has studied their acoustical behaviour and reproductive isolation (McIntyre 1974, 1977).

In this paper, the distribution and habits of *P. nigrovus* and *P. bigelowi* are discussed and the results of experiments on egg incubation time and hatching success of crickets from two South Island localities Kaikoura (42°24'S, 173°41'E) and Christchurch (43°33'S, 172°40'E) are reported.

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DISTRIBUTION AND HABITAT

Pteronemobius nigrovus and *P. bigelowi* are found throughout most of lowland New Zealand (Swan 1972, Hudson 1973, McIntyre 1974). Both species have been recorded at an altitude of 1 895 m (Swan 1972), but apart from occasional pockets of sheltered grassland, this appears to be exceptional and generally they are not abundant above 1 000 m. They are frequently sympatric, *P. bigelowi* appears to be predominant in the north of the North Island whereas *P. nigrovus* increases in relative abundance further south and predominates in the south of the South Island and in sub-alpine areas. My observations indicate that the seasonal abundance of both species varies, and their distributions tend to be patchy with very high local densities in late summer and autumn.

Differences between the species are evident in seasonal changes in their relative abundance at some locations, and also to some extent in their distributional patterns. At Christchurch *P. nigrovus* are often abundant from February until April, but I found only two individuals of *P. bigelowi* during these months, Swan (1972) found none and Wilkinson (1970) did not mention them. In August and September I have found very few crickets at Christchurch but about half were *P. bigelowi* whereas at Hunterville, in the southern half of the North Island, the species occur in about equal proportions throughout most of the year, although total numbers are much lower in the second half.

Only *P. bigelowi* has been recorded at Kaikoura and adults are present there from late January until June, by which time numbers have declined considerably. Parkes (1972) found a single annual generation (apparently only *P. bigelowi*) at Hamilton with an obligate winter egg diapause; nymphs were present in the field from mid-October to about April, and adults from mid-February to early November. However at Kawhia, a nearby coastal location, both nymphs and adults occurred throughout the year with little evidence of diapause.

Both species show a distinct preference for moist situations in short to medium height grasses which are unmown or lightly grazed. They do not seem to move readily through thick, tall vegetation, although some crickets may be found on tall grasses where there is sufficient space for movement among stems, or if the grass is flattened into a mat which they can climb over. Their small size enables them to move easily beneath the layer of litter which typically covers grassland soils, and this probably accounts for their apparent disappearance in unfavourable weather conditions. In bright sunlight they tend to move out near the tips of vegetation. Kirby (1968) found that they will accept a wide range of herbaceous food material, and Swan (1972) suggested that decaying matter may also form a significant part of their diet.

INCUBATION AND HATCHING

METHODS

Crickets collected from Christchurch *(P. nigrovus)* and Kaikoura *(P. bigelowi)* in February and March 1969 were used as a source of eggs for laboratory experiments. They were in groups of six females and four males with "sheepnuts" (a commercial stockfood) for food and open petri dishes of moist "perlite" (a commercial plant substrate) for oviposition. The latter also satisfied humidity needs. Crumpled newsprint provided shelter and had the additional effect of spacing out the crickets, thereby reducing both aggression among males and fouling of containers. Crickets were anaethetised with carbon dioxide before handling.

Perlite was washed and decanted off every three to four days for 70 days and all eggs were removed from the residue. Eggs of each species were divided into four groups, A-D, which were placed on moist Plaster of Paris in plastic petri dishes, and each group was incubated as indicated in Table 1. The dishes were placed inside moistened plastic bags to prevent drying out. This procedure was repeated each time eggs were collected. Observations of egg incubation were discontinued after 180 days, although some eggs may still have been viable at that time.

TABLE 1. INCUBATION TREATMENTS.

Treatment	Conditions	Numbers of eggs in each treatment	
		P. nigrovus	*P. bigelowi*
A	26-29°C	219	307
B	room temperature	760	146
C	24 h at 4°C; then 26-29°C	224	311
D	12 h at -7°C; then 26-29°C	224	306

In March and April 1970 more eggs of *P. nigrovus* from Christchurch and *P. bigelowi* from Kaikoura were collected at 3-4 day intervals as above and held at room temperature. After 56 days 250 eggs of each species were examined for indications of diapause. Eggs of *P. nigrovus* were treated using the method of Hogan (1959) to remove the black chorion thereby making the contents visible but this was unnecessary with *P. bigelowi* eggs.

Finally eggs collected from both species at Christchurch in August and September 1973 (about 300 of each species) were incubated at 27°C on Plaster of Paris and examined daily for 2 weeks.

RESULTS

Females of both species oviposit over a period of 2-3 months and deposit eggs below the surface of moist soil at depths of up to 5 mm. Eggs of *P. nigrovus* are

black and heavily sclerotised, the pigmentation developing just prior to or during oviposition. Eggs of *P. bigelowi* are not heavily sclerotised and are translucent creamy-white although they may darken if they become non-viable. My observations showed that the eggs of both species require moist conditions for development, and those of *P. bigelowi* in particular seem sensitive to desiccation during diapause. Viable eggs swell shortly after oviposition and lose their turgidity after becoming non-viable. During incubation, some *P. nigrovus* eggs kept at room temperature were accidentally allowed to dry, but some of these hatched subsequently suggesting that they may be more tolerant to desiccation than those of *P. bigelowi* which collapsed rapidly in a dry atmosphere.

The hatching frequency and incubation periods of eggs in each of the four temperature treatments are shown in Fig. 1. Although the percentage hatch was low (*P. nigrovus* 4.9%, n=1 427; *P. bigelowi* 9.6%, n=1 070), it differed

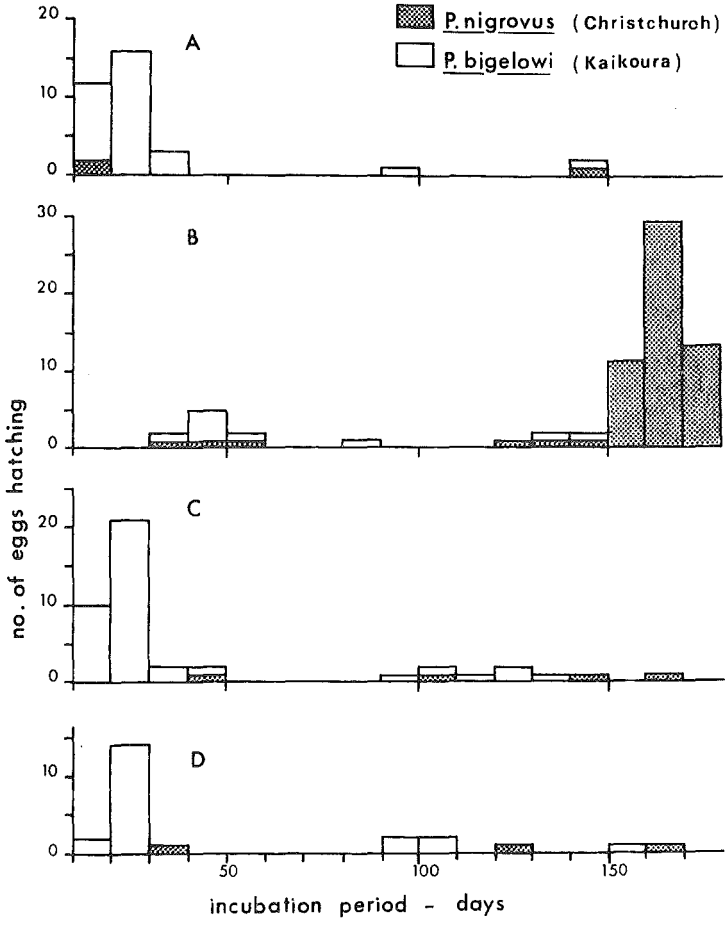

FIG. 1. Hatching frequency and incubation periods of eggs of *P. nigrovus* and *P. bigelowi*. (A,B,C,D as in Table 1).

significantly between the species ($t=3.09$, $P < 0.05$), but not between treatments ($F=0.08$, $P > 0.2$). The differences between the incubation period of the two species suggest that the eggs possess inherent differences in sensitivity to external factors. It appeared that most *P. nigrovus* eggs from Christchurch entered an intense state of diapause which was little affected by the warm (Fig. 1A) or cold (Fig. 1C, 1D) temperatures to which they were exposed, and that most of those developing at room temperature (Fig. 1B) represented a post-diapause hatch. On the other hand, eggs of *P. bigelowi* from Kaikoura were affected more readily by the incubation treatments, indicating that either diapause was less intense (eggs more sensitive to external factors) in *P. bigelowi* at this location (Fig. 1C, 1D) than in *P. nigrovus* from Christchurch at this time of year or that it involved a smaller proportion of eggs (Fig. 1A).

The numbers of eggs found at various stages of embryonic development after being held at room temperature for up to 56 days are shown in Table 2. Most eggs of both species (80.6%) had reached a similar stage of development in

TABLE 2. DEVELOPMENTAL STAGES AFTER UP TO 56 DAYS AT ROOM TEMPERATURE.

Developmental stages	Numbers of eggs	
	P. nigrovus	*P. bigelowi*
inviable (shrivelled)	24	1
infertile (clear)	32	19
diapause (cell mass)	190	213
early development (eyespot)	1	6
advanced embryo	3	11
total	250	250

which a small apparently homogeneous mass of cells was suspended in a clear liquid. Since these varied in incubation time but had apparently reached a similar stage of development, it was concluded that development had been suspended and they had entered a state of diapause. Of the remaining eggs some (10.2%) were completely clear and probably infertile (Swan 1972), whereas others (4.2%) had advanced to a stage where eyespots were visible and these had presumably either continued or resumed development. Eggs of *P. bigelowi* at 27°C usually hatched 10-14 days after reaching the eyespot stage. These results corroborate the suggestion of Swan (1972) that the eggs of both species enter diapause at an early embryonic stage, and suggest that a high proportion of eggs will enter diapause before the onset of winter at both Christchurch and Kaikoura.

DISCUSSION

Swan (1972) suggested that both *P. nigrovus* and *P. bigelowi* have univoltine life cycles with egg diapause. My observations

and those of Wilkinson (1970) and Parkes (1972) indicate that the life cycles are subject to local variation and there may be ecological differences between the species.

Diapause in these crickets appears to be primarily a device to escape winter cold, (the eggs being responsive to certain temperature factors, which can be manipulated to some extent to induce hatching). The eggs show both intraspecific and interspecific variation in their capacity for diapause. At Christchurch Wilkinson (1970) obtained a 51.5% hatch for *P. nigrovus* eggs collected in February and March and held four weeks at 4-7°C; this increased to 83.5% for eggs held for eight weeks at the same temperature, but declined to 6.5% when held for 24 hours at -5°C to -7°C. Similarly Swan (1972) found that 80% of *P. nigrovus* eggs obtained at Christchurch in February hatched after eight weeks at 5°C-9°C. It seems that these eggs were relatively insensitive to short term temperature changes and required lengthy exposure to cold but not freezing conditions to stimulate a large hatch. By contrast, both species of crickets collected from the same areas in August and September (Author's unpublished data) produced eggs, 90% of which hatched apparently without diapause; after 11-14 days at 27°C. Mr B. Johnstone (Department of Zoology, University of Otago, pers. comm. 1971) also noted that the eggs of *P. nigrovus* collected from North Otago during March and April required at least 20 days at 6°C to stimulate hatching, whereas eggs collected there in July and August required only five days.

It is possible that the black *P. nigrovus* eggs, with their protective chorion and stronger diapause, are a more effective overwintering stage than the seemingly more delicate eggs of *P. bigelowi*. In addition, the longer ovipositor of *P. nigrovus* females (Swan 1972) enables deeper placement of eggs in the soil. Also adults of *P. bigelowi* may overwinter effectively, at least as far south as Christchurch (Swan 1972) so that the unprotected egg with its weaker diapause does not exclude this species from such areas. Bigelow and Cochaux (1962) and Bigelow (1963) have similarly reported that the eggs of *Teleogryllus* spp., in Australia and New Zealand respectively, enter diapause in varying proportions according to seasonal factors and location.

In areas which have a long season for active growth and where seasonal climatic differences are small, as in northern New Zealand and some coastal locations the intensity of diapause and proportions of diapause eggs found can be expected to remain constantly low, and in mild equable conditions to approach zero. In contrast, where seasonal differences preclude continuous growth a single annual generation with approaching 100% winter diapause is more likely to be found. At such locations some adults may continue to mate and produce eggs over the winter, but

both the tendency of these eggs to enter diapause and the intensity of diapause decrease (i.e. sensitivity to external factors increases) from autumn to spring synchronizing the appearance of nymphs in the field when conditions are most favourable for their development. This appears to be the case for Christchurch and Otago cricket populations.

Overall it would appear that selection has maintained flexibility in the capacity of each species to enter diapause in response to environmental factors. It follows that egg diapause in these species must be regulated by a polygenic system whose expression can be modified by non-genetic (environmental) factors as has been postulated for other cricket species (Bigelow 1962, 1963). These environmental factors may be long term changes in photoperiod and/or temperature which have a cumulative effect on maturing females, causing diapause in the eggs produced to vary in occurrence, duration and intensity. The seemingly obligate condition in some populations may then represent a high frequency of diapause occurrence which is maintained where this is of value. Diapause also persists at some northern and coastal locations where it has little apparent value in relation to winter climates. This could be due to the establishment of diapause factors in the gene system of the species under past conditions.

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